NRC Research Press

REVIEW

Fire and dwarf mistletoe (Viscaceae: *Arceuthobium* species) in western North America: contrasting *Arceuthobium tsugense* and *Arceuthobium americanum*[1]

David C. Shaw and Michelle C. Agne

Abstract: Dwarf mistletoes (Viscaceae: *Arceuthobium* spp.) and fire interact in important ways in the coniferous forests of western North America. Fire directly affects dwarf mistletoes by killing the host, host branch, or heating/smoking the aerial shoots and fruits. Fire is a primary determinant of dwarf mistletoe distribution on the landscape, and time since fire controls many aspects of dwarf mistletoe epidemiology. Conversely, dwarf mistletoes can influence fire by causing changes in forest composition, structure, and fuels. Prescribed fire is important for management of dwarf mistletoes, while fire suppression is thought to have increased dwarf mistletoe abundance in western forests. Two dwarf mistletoes are compared in order to illustrate fire interactions in Oregon and Washington, USA: *Arceuthobium americanum* Nutt. ex Engelm. (lodgepole pine dwarf mistletoe) and *Arceuthobium tsugense* (Rosendahl)(western hemlock dwarf mistletoe). *Arceuthobium* persists on the landscape where the host is not killed by fire. *Arceuthobium americanum* spreads directly into the regenerating *Pinus contorta* Dougl. ex Loud., while *A. tsugense* persists in refugia for 200 years or more following fire. Host successional status is a driver of fire – dwarf mistletoe interactions, but forest disturbance agents also play a role. Given the importance of these interactions to the ecology of fire-prone forests, dwarf mistletoes warrant inclusion in disturbance ecology research.

Key words: Arceuthobium spp., coniferous forests, disturbance interactions, dwarf mistletoe, fire ecology.

Résumé : Le faux-gui (Viscaceae : *Arceuthobium* spp.) et le feu interagissent de manière importante dans les forêts de conifères de l'ouest de l'Amérique du Nord. Le feu affecte directement le faux-gui en tuant l'hôte, les branches de l'hôte ou en chauffant/enfumant les systèmes foliacés et les fruits aériens. Le feu est le principal déterminant de la distribution du faux-gui dans le paysage et le temps écoulé depuis un incendie contrôle plusieurs aspects de l'épidémiologie du faux-gui. Inversement, le faux-gui peut influencer le feu en provoquant des changements dans la composition, la structure et les combustibles de la forêt. Le brûlage dirigé est important à la gestion du faux-gui, alors que l'on croit que la suppression des incendies accroit l'abondance du faux-gui dans les forêts de l'ouest. Deux espèces de faux-gui sont comparées afin d'illustrer leurs interactions avec le feu dans les états de l'Oregon et de Washington, USA : *Arceuthobium americanum* Nutt. ex Engelm. (faux-gui du pin lodgepole) et *Arceuthobium tsugense* (Rosendahl)(faux-gui de la pruche de l'ouest). *Arceuthobium* persiste dans le paysage où l'hôte n'est pas tué par le feu. *Arceuthobium americanum* se propage directement sur *Pinus contorta* Dougl. ex Loud. en régénération, alors que *A. tsugense* persiste dans des refuges pendant 200 ans et plus après un feu. L'état sérial de l'hôte est un moteur des interactions feu — faux-gui, mais les agents perturbant la forêt jouent aussi un rôle. Compte tenu de l'importance de ces interactions dans l'écologie des forêts susceptibles aux feux, le faux-gui mérite d'être inclus dans la recherche portant sur l'écologie de la perturbation. [Traduit par la Rédaction]

Mots-clés : Arceuthobium spp., forêts de conifères, interactions perturbatrices, faux-gui, écologie du feu.

Introduction

Dwarf mistletoes (Viscaceae; *Arceuthobium* spp.) are parasitic flowering plants that infect conifers in the Pinaceae in North America, as well as *Juniperus* and *Cupressus* spp., and other Pinaceae from northern Africa, southern Europe, and China (Hawksworth and Wiens 1996; Geils et al. 2002; Mathiasen et al. 2008). These plants interact with host trees to influence crown structure and forest fuels particularly in dry forests of western North America (Wicker and Leaphart 1974). The interactions of fire and dwarf mistletoe have been noted for some time (Roth 1953; Hawksworth 1961), but in the 1970s, several papers brought

---

Received 2 September 2016. Accepted 20 October 2016.

D.C. Shaw and M.C. Agne. Department of Forest Engineering, Resources, and Management, 218 Richardson Hall, Oregon State University, Corvallis, OR 97331, USA.

Corresponding author: David C. Shaw (email: dave.shaw@oregonstate.edu).

[1] This Review is part of a Special Issue from the 2016 IUFRO Conference: Mistletoes: Pathogens, Keystone Resource, and Medicinal Wonder.

Botany **95**: 231–246 (2017) dx.doi.org/10.1139/cjb-2016-0245

the importance of these dynamics to wider recognition. Irving and French (1971) demonstrated that prescribed fire can be used to control dwarf mistletoe in a paper that detailed a method of burning an infection center using diesel fuel and tree felling to form continuous fuels and kill all host trees. Wicker and Leaphart (1974) discussed four common host – dwarf mistletoe interactions with fire in the Northern Rockies, and Alexander and Hawksworth (1976) synthesized knowledge of fire and dwarf mistletoe interactions broadly. They emphasized that fire was the most important natural control on the distribution and abundance of dwarf mistletoe in North American conifer forests, that fire suppression had increased infection levels on the landscape, and noted that there was a general lack of data on the subject. More recently, Shaw et al. (2004*a*), Parker et al. (2006), and Muir and Hennon (2007) included discussions of the interactions between fire and dwarf mistletoe, although this was not the main focus of these publications.

Alexander and Hawksworth (1975, 1976) considered that wildfire can affect dwarf mistletoe populations in either an adverse or beneficial way. Fire kills host trees and dwarf mistletoe plants (which require a living host), influencing landscape pattern and limiting the severity of infections as well as potential for spread. However, fire can also maintain a host on the landscape. For example, in the northern Rocky Mountains, lodgepole pine (*Pinus contorta* Dougl. ex Loud.) is an early successional species and a host for lodgepole pine dwarf mistletoe (*Arceuthobium americanum* Nutt. ex Engelm.). Fire prevents succession to the late seral species, Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) and subalpine fir (*Abies lasiocarpa* [Hook.] Nutt.), which are not primary hosts for any *Arceuthobium* species. In this way, fire can aid dwarf mistletoe by preventing nonhost dominance. Although fire influences dwarf mistletoe, the effect of dwarf mistletoe on individual tree and stand structure may increase ladder fuels and flammability of trees due to witches' brooms, litter accumulation in the crown, dead branch, and crown structures, and associated surface fuels from mortality, which may influence fire behavior, especially the potential for torching (Wicker and Leaphart 1974; Fig. 1).

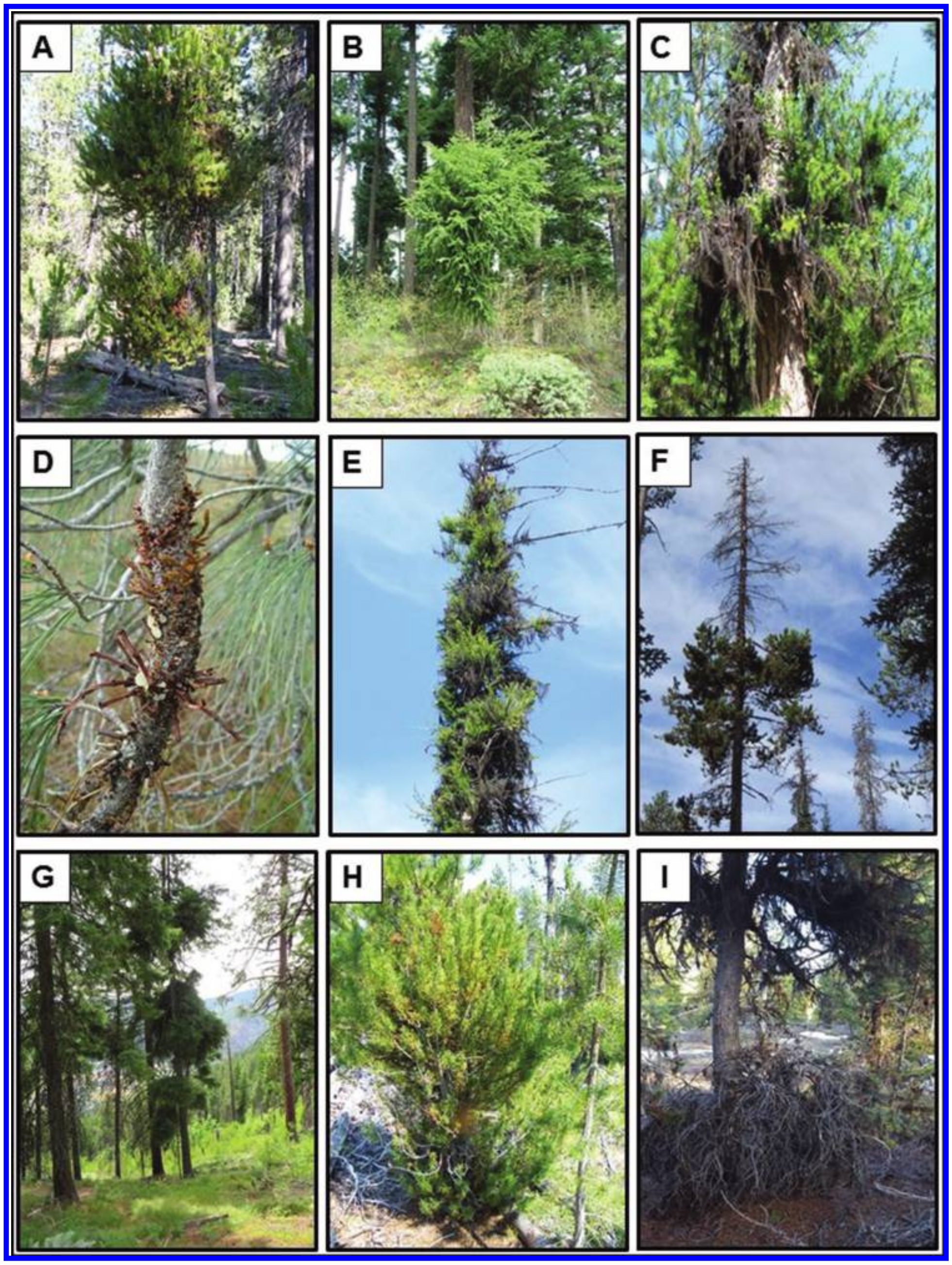
Since these papers, research has been sparse on fire and dwarf mistletoe interactions, but can be divided into three general categories: fire's influence on dwarf mistletoe, dwarf mistletoe's influence on fuels, fire behavior, and fire severity, and use of prescribed fire to control dwarf mistletoe. The objectives of this paper are as follows: (*i*) briefly review the literature on fire and dwarf mistletoes in western North America, and (*ii*) contrast two ecologically distinct dwarf mistletoes, *Arceuthobium tsugense* (Rosendahl) G.N. Jones and *A. americanum*, and their different relationships with fire in the Pacific Northwest region of the USA to emphasize the importance of fire in *Arceuthobium* ecology. In this comparison, we rely on published research from Wind River Experimental Forest (Shaw and Greene 2003) to characterize *A. tsugense*'s relationship with fire, and a combination of previously published research and new analyses from central Oregon in the examination of *A. americanum*'s relationship to fire. The interrelationships between *P. contorta*, fire, and dwarf mistletoe are also intimately tied to dynamics of mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks in this system, such that dwarf mistletoe effects on fuels must be examined while accounting for the effects of mountain pine beetle (Agne et al. 2014). New analyses addressed the research questions: (*i*) How does *A. americanum* severity change following the mountain pine beetle epidemic? (*ii*) How does *A. americanum* influence fuels in post-mountain pine beetle stands? (*iii*) How does fire influence *A. americanum* incidence and severity in stands which had experienced a mountain pine beetle epidemic prior to fire?

Fire's influence on dwarf mistletoe

Fire can influence the distribution and severity of dwarf mistletoe on the landscape through multiple mechanisms (Wicker and Leaphart 1974). The first mechanism by which fire may control dwarf mistletoe is through direct exposure of the dwarf mistletoe plant to fire. Direct exposure of seeds to heat and smoke is thought to be one of the key drivers of *Arceuthobium* fecundity and seed germination (Alexander and Hawksworth 1976). Zimmerman and Laven (1987) tested the effects of smoke generated from burning forest fuels on seed germination of three species of dwarf mistletoe (*A. americanum, Arceuthobium cyanocarpum* (A. Nelson ex Rydberg) Coulter and Nelson, and *Arceuthobium vaginatum* (Willd.) Presl subsp. *cryptopodum* [Engelm.] Hawksw. & Wiens) by exposing seed to smoke in a controlled lab environment. They found that germination was generally not inhibited until 30 min of exposure, and germination of *A. americanum* seed was actually enhanced by 30 min of exposure to smoke from dry fuels. After 60 min, seed germination of all three species was almost entirely inhibited. Further research surrounding interactions of *Arceuthobium* germination and fire is needed, as this is the only study we are aware of which addresses this subject.

The second mechanism of dwarf mistletoe control by fire is through exposure of the host to heat from fire. The influence of fire on dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum*) infections and infected trees was studied in ponderosa pine (*Pinus ponderosa* Dougl. ex P. Laws. & C. Laws.) in Arizona after prescribed fire in natural uneven-aged stands (Harrington and Hawksworth 1990). They used the Hawksworth 6-class dwarf mistletoe rating (DMR) system to rate dwarf mistletoe severity (Hawksworth 1977), where a tree crown is divided into vertical thirds and each third is rated 0 if no dwarf mistletoe occurs, 1 if <50% of the branches have infections, and 2 if >50% of the branches have infections. The ratings of third are summed, and a DMR of 6 is possible for the most severely infected trees. They concluded that amount of crown

Fig. 1. Illustrated guide to fuel structures caused by host – dwarf mistletoe interactions in western North America. (A) Witches' brooms in *Pinus contorta* caused by *Arceuthobium americanum*. (B) Witches' broom in *Pseudotsuga menziesii* caused by *Arceuthobium douglasii*. (C) Litter and lichen accumulation in *Larix occidentalis* witches' broom caused by *Arceuthobium laricis*. (D) Resin soaked branches of *Pinus sabiniana* associated with *Arceuthobium occidentale*. (E) Dead branches and crown top in *Larix occidentalis* associated with *Arceuthobium laricis*. (F) Dead crown top on *Pinus contorta* associated with *Arceuthobium americanum* infections. (G) Lowered canopy base height in *Pseudotsuga menziesii* associated with *Arceuthobium douglasii* witches' brooms. (H) Heavily infected understory *Pinus contorta* with no apical dominance, and which is essentially one *Arceuthobium americanum* broom. (I) Surface fuel accumulation at base of *Pinus contorta* associated with *Arceuthobium americanum*. [Colour online.]



scorched by fire increased with increasing DMR, and that given an intermediate amount of crown scorch, heavily infected trees were more likely to die than uninfected trees. Therefore, fire reduced dwarf mistletoe rating within stands by killing heavily infected hosts, and heavy dwarf mistletoe infection led to increased fire severity. Queijeiro-Bolaños et al. (2013) also determined that there is a negative association between *A. vaginatum* subsp. *cryptopodum* presence and distance to a burned area in the *Pinus hartwegii* Lindl. stands of central Mexico.

A combination of both mechanisms described above likely facilitates the negative association between time since fire and dwarf mistletoe rating. This relationship has been shown in particular for *A. americanum* in lodgepole pine forests, with considerably lower rates of infection in recently burned areas than in areas that have not burned in centuries (Hawksworth and Johnson 1989). Zimmerman and Laven (1984) found that stand level dwarf mistletoe rating decreased with increased fire frequency in lodgepole pine in southwestern Colorado. Kipfmueller and Baker (1998) used a landscape scale approach to investigate the influence of fire on *A. americanum* in the lodgepole pine forests of the Medicine Bow Mountains of Wyoming. They found that dwarf mistletoe occurred in 51% of the stands investigated, and that stand level infection rating generally increased with increased time since fire. Survival of individual trees following fire also increased the likelihood of dwarf mistletoe infestation in a forest stand. They also observed that heavily infected stands with distinct infection centers had a large influence on landscape spatial patterns, and suggest that dwarf mistletoe slowly spreads from these centers. Dwarf mistletoe was not ubiquitous; therefore high-severity fire may play a significant role in eradicating dwarf mistletoe from some areas. The patchy distribution of fire may prevent high intensity dwarf mistletoe infection centers from dominating the landscape.

Dwarf mistletoe's influence on fuels, fire behavior, and fire severity

Dwarf mistletoe influences fuels characteristics in forests, and this is thought to influence subsequent fire behavior. However, data are limited or based on anecdotal observations and fire behavior models not intended for evaluation of stands with dwarf mistletoe. Dwarf mistletoe infected trees generally have distinctive crown characteristics that influence fuels including: witches' brooms and associated litter accumulations within brooms, dead branches with persistent fine materials, dead tops, resin soaked branches, lowered canopy base height due to persistence of witches' brooms in the lower crown, heavily infected understory trees that lose apical dominance, and whole tree mortality (Fig. 1; Wicker and Leaphart 1974; Alexander and Hawksworth 1976; Hawksworth and Wiens 1996).

Dwarf mistletoe's influences on fuel loadings have been best studied in ponderosa pine forests but overall results are equivocal. Hoffman et al. (2007) studied the effects of *A. vaginatum* subsp. *cryptopodum* on fuel loadings in ponderosa pine forests in northern Arizona. They found that stands with severe dwarf mistletoe had lower tree density, higher snag density, and greater surface fuel and total fuel loadings. Koonce and Roth (1985) found that fine surface fuels increased and crown base heights decreased in severely infected Oregon ponderosa pine stands as compared with uninfected and lightly infected stands. Stanton and Hadley (2010) found a weak influence of dwarf mistletoe on fine surface fuels in central Oregon ponderosa pine forests, although this effect varied with factors like stand density or species composition. Stanton (2009) found little influence of dwarf mistletoe on fuels structure in ponderosa pine at Crater Lake National Park, Oregon.

The influence of dwarf mistletoe infection intensity on fire behavior using models or field-based observational data has been rarely studied. Although Hoffman et al. (2007) found no difference in modeled fire rate of spread, fireline intensity, or flame length associated with dwarf mistletoe, they found that lower wind speeds were required for surface fires to transition into the canopy in dwarf mistletoe-infected ponderosa pine stands than in uninfected stands. However, the assumptions of currently available operational fire behavior models are not necessarily appropriate for modeling fire behavior in disturbed stands (Cruz and Alexander 2010) and it is unclear whether model results from dwarf mistletoe infected forests are representative of in situ fire behavior. In a case study at Crater Lake National Park, Stanton (2009) found that observed fire behavior was similar in ponderosa pine stands with and without dwarf mistletoe, although infected stands burned at high temperatures for shorter durations than did uninfected stands, potentially altering the consumption of woody fuels and residual fuel loadings following fire. Additionally, witches' brooms were potentially more flammable than uninfected branches, although more research is needed to confirm this relationship.

The influence of dwarf mistletoe on fire severity and post-fire survival has been occasionally studied. Turner et al. (1999) studied the lodgepole pine forests in Yellowstone National Park after the 1988 fires to determine the influence of pre-fire spatial heterogeneity on fire severity. They found that pre-fire disturbance by mountain pine beetle and *A. americanum* played a role in fire severity. Stands most severely affected by the insect or dwarf mistletoe had a higher likelihood of crown fire, while stands with intermediate damage were less likely to have crown fire. Additionally, Harrington and Hawksworth (1990) found that crown scorch was more likely in heavily infected ponderosa pine than uninfected ponderosa pine in Arizona, and an uninfected tree was more likely than an infected tree to survive similar level of crown scorch. Similarly, Conklin and Geils (2008) found that average crown scorch was higher in heavily infected trees than in uninfected to lightly infected ponderosa pine in New Mexico. They also noted that post-fire survival decreased in heavily infected trees. It should be noted that the vast majority of research on the influence of dwarf mistletoe on fuels, fire behavior, fire severity, and post-fire tree survival has been conducted in ponderosa pine forests. Although it appears that ponderosa pine dwarf mistletoe influences these attributes in ponderosa pine to various extents, it is unknown whether other dwarf mistletoes associated with other forest types have similar effects.

It is important to note that dwarf mistletoe does not act alone as a biotic disturbance agent in western forests (Parker et al. 2006). Klutsch et al. (2014) demonstrated that the combined effects of bark beetles (mountain pine beetle and *Ips* spp. [Coleoptera: Curculionidae: Scolytinae]) and dwarf mistletoe (*A. vaginatum* subsp. *cryptopodum*) have a strong influence on downed woody fuel loading, biomass accumulation, fuel arrangements, stand density, and species composition in ponderosa pine forests of Colorado. Root and butt rot fungi as well as mountain pine beetle interact to influence fire behavior and patterns in *Pinus contorta* forests of central Oregon (Geiszler et al. 1980), and these agents surely influence patterns of *A. americanum* distribution. Furthermore, mortality of branches infected with *Arceuthobium* spp., and therefore dead canopy fuels, may increase during drought, owing to reduced water use efficiency (Sala et al. 2001; Meinzer et al. 2004). This interaction may become more pronounced in the future, given predictions for increased drought in western North America (Allen et al. 2015).

Prescribed fire and dwarf mistletoe control

Prescribed fire is known to aid in the control of dwarf mistletoes, but unless all trees are killed, fire will only aid to control, not eradicate dwarf mistletoe (Irving and French 1971; Alexander and Hawksworth 1976). Prescribed fire that reduces dwarf mistletoe immediately following fire has been documented in lodgepole pine forests of British Columbia (Muraro 1978), ponderosa pine forests in Oregon (Koonce and Roth 1980), Arizona (Harrington and Hawksworth 1990), and New Mexico (Conklin and Geils 2008), as well as dry mixed-conifer forests in Washington (Hessburg et al. 2008) and California (Maloney et al. 2008). Prescribed fire aids control of dwarf mistletoe by killing witches' brooms and aerial shoots in the lower crown, killing infected trees, removing infected regeneration and understory trees, and reducing total stand density. In combination with thinning, this approach can be very effective at managing dwarf mistletoe, with modeled treatment effects lasting up to 100 years in dry mixed-conifer stands in Washington (Hessburg et al. 2008). Conklin and Geils (2008) estimated that a prescribed fire with 50% scorch and initial average stand dwarf mistletoe rating of 3 will reduce the stand dwarf mistletoe rating by 0.7 for at least three years following fire. Alternatively, Irving and French (1971) showed that dwarf mistletoe infection centers can be eradicated with some tree felling to form a continuous fuel bed. Prescribed burning was shown to slightly reduce dwarf mistletoe severity in mixed conifer forests of the Sierra Nevada Mountains, California immediately following treatment (Maloney et al. 2008). However, spread and intensification rates were not projected to be significantly altered when projected over the 50 years following treatment. Additionally, they found that fire damage following prescribed burning was highly correlated with dwarf mistletoe infected trees, suggesting that infected trees are more likely to be killed by prescribed fire than uninfected trees.

Contrasting the fire ecology of *Arceuthobium tsugense* (western hemlock dwarf mistletoe) and *Arceuthobium americanum* (lodgepole pine dwarf mistletoe)

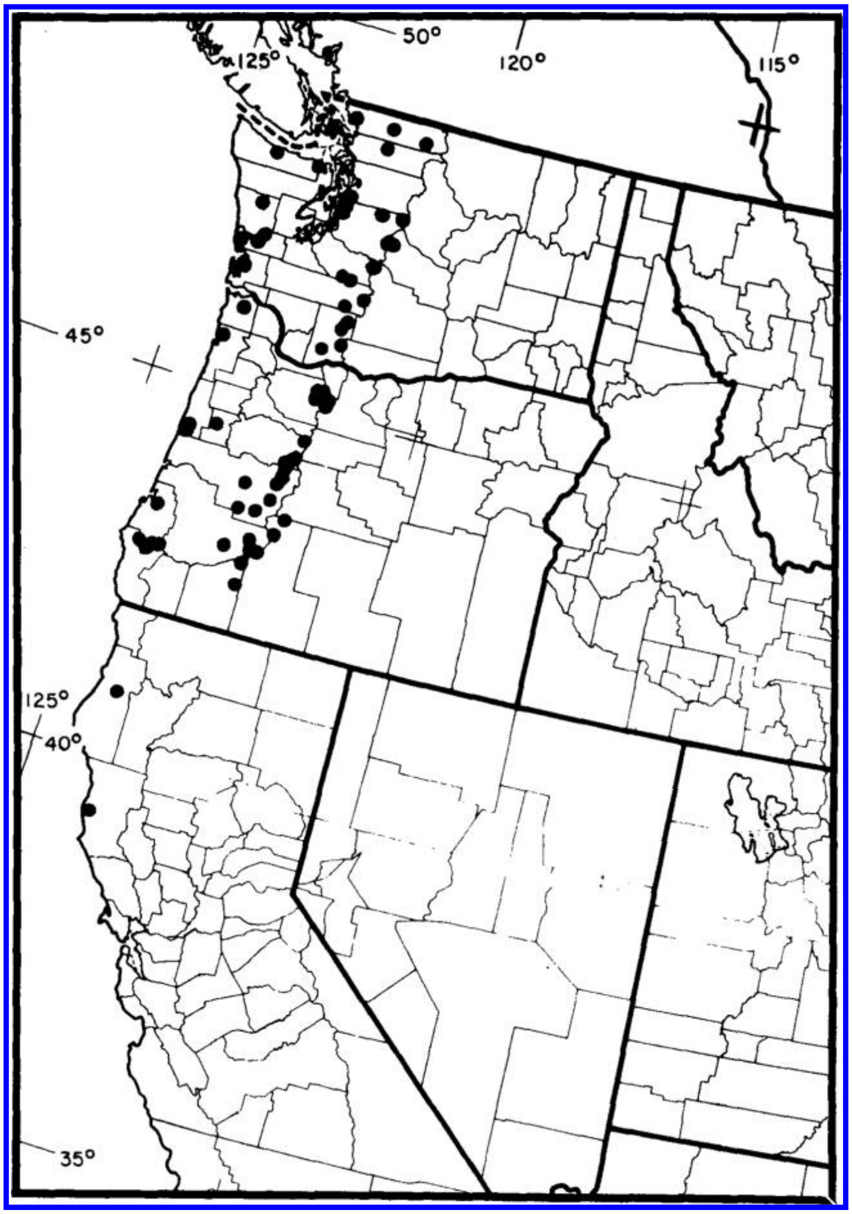
Western hemlock dwarf mistletoe in the western hemlock forests of the southern Washington Cascade Mountains, USA

Western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) is a host *to A. tsugense* (Hawksworth and Wiens 1996; Muir and Hennon 2007) in the Douglas-fir (*Pseudotsuga menziesii* [Mirb. Franco]) and *T. heterophylla* forests that dominate northwest Oregon and western Washington up to 1500 m elevation (Franklin and Dyrness 1973). The range of *A. tsugense* is limited to west of the crest of the Cascade Mountains (Fig. 2; Hawksworth and Wiens 1996). *Tsuga heterophylla* is a late-successional species, which typically does not become dominant in a stand until after several hundred years. Therefore the region is largely dominated by *P. menziesii*, except in hypermaritime and very old (>300 years) stands in national forests, national parks, and wilderness areas. Although wind is the primary disturbance factor that interacts with *A. tsugense* in coastal forests (Trummer et al. 1998; Muir and Hennon 2007), fire is the primary natural determinant of forest age and structure in the western Cascades region. This forest type is characterized by a high severity, stand replacement fire regime and long fire return interval, averaging 230 years, and increasing with elevation and rainfall (Franklin and Dyrness 1973; Agee 1993).

Franklin et al. (2002) described the structural succession of this forest type with eight distinctive developmental stages: (1) disturbance/legacy creation; (2) cohort establishment, (3) canopy closure, (4) biomass accumulation/competitive exclusion, (5) maturation, (6) vertical diversification, (7) horizontal diversification, (8) pioneer cohort loss. *Pseudotsuga menziesii* dominates the first six stages, and *T. heterophylla* becomes a significant component of the canopy in the last three stages, after 250–300 years or longer, depending on elevation, site productivity and severity of the previous stand replacement fire. Research reported here on *A. tsugense* was conducted in the southern Cascade Mountains of Washington state where natural forests are dominated by two age classes: a 450 year old-growth *P. menziesii* and *T. heterophylla* forest in the horizontal diversification phase, and a 157 year old *P. menziesii* forest in the maturation phase, that regenerated naturally from fire disturbance.

Crown structure and characteristics of fuels are influenced by dwarf mistletoe in western hemlock, although no data exists on changes in canopy bulk density or canopy base height. Infections by *A. tsugense* may cause formation of witches' brooms that are distinct structures of flattened, dense profuse branching with no apical dominance, that continue to enlarge indefinitely (Hennon et al. 2001; Muir and Hennon 2007). The majority of infected trees in the 450 year old south Washington Cascades forest had brooms in the lower crowns, potentially influencing fuels organization in live trees (Shaw et al. 2005). *Pseudotsuga menziesii* dominated the canopy from about

Fig. 2. Distribution map of *Arceuthobium tsugense* subsp. *tsugense*, in Oregon, Washington, and California (from Hawksworth and Wiens 1996). Available online at http://www.treesearch.fs.fed.us/pubs/4699.

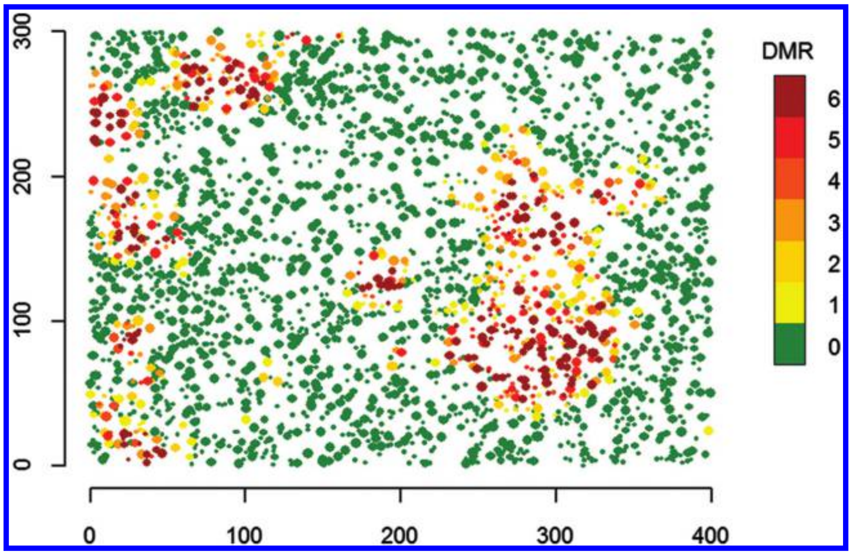


35–60 m, while *T. heterophylla* crowns dominated the canopy from 5 to 35 m and larger *T. heterophylla* were more likely to be infected by *A. tsugense* than small trees. A majority of infected trees had dwarf mistletoe-caused brooms in the lower, middle, and upper crown, with lesser numbers of trees with brooms only in the middle and lower crowns. In addition, Meinzer et al. (2004) found that whole tree water use was lower in heavily infected trees compared with uninfected trees because of reduced numbers of live branches. Large numbers of dead, witches' brooms occurred throughout heavily infected trees, creating crowns with mixed live and dead fine fuels of varying size classes.

A 12 ha stem-mapped research plot was established in a 450 year old *P. menziesii*/*T. heterophylla* forest with significant *Thuja plicata* Donn ex D. Don component (Shaw et al. 2004*b*; Chen et al. 2004) and *A. tsugense* distribution was mapped (Shaw et al. 2005) using the Hawksworth 6-class dwarf mistletoe rating (DMR) system (Hawksworth 1977). *Arceuthobium tsugense* occurred in distinct infection centers in which heavily infected trees (DMR 6) were most likely to be near other infected trees, and lightly infected trees were most likely near uninfected trees, indicating contagion with spread from infection centers (Fig. 3; Shaw et al. 2005). However, some lightly infected trees were greater than 30 m from other infected trees (Fig. 3), indicating the possibility that birds or other animals could be assisting movement of seed.

The patchy distribution of *A. tsugense* on the landscape is a well-known characteristic in *T. heterophylla* forests (Hennon et al. 2001; Muir and Hennon 2007). There were eight locations of clumped DMR 6 trees within the

Fig. 3. Distribution of *Tsuga heterophylla* by dwarf mistletoe rating (green = 0, magenta = 6), on a 12 ha plot in old-growth *Pseudotsuga menziesii* – *Tsuga heterophylla* forest in the T.T. Munger Research Natural Area, Wind River Experimental Forest, Washington State. Map by Elizabeth Freeman, reproduced with permission from Shaw et al. (2009), data from Shaw et al. (2005).



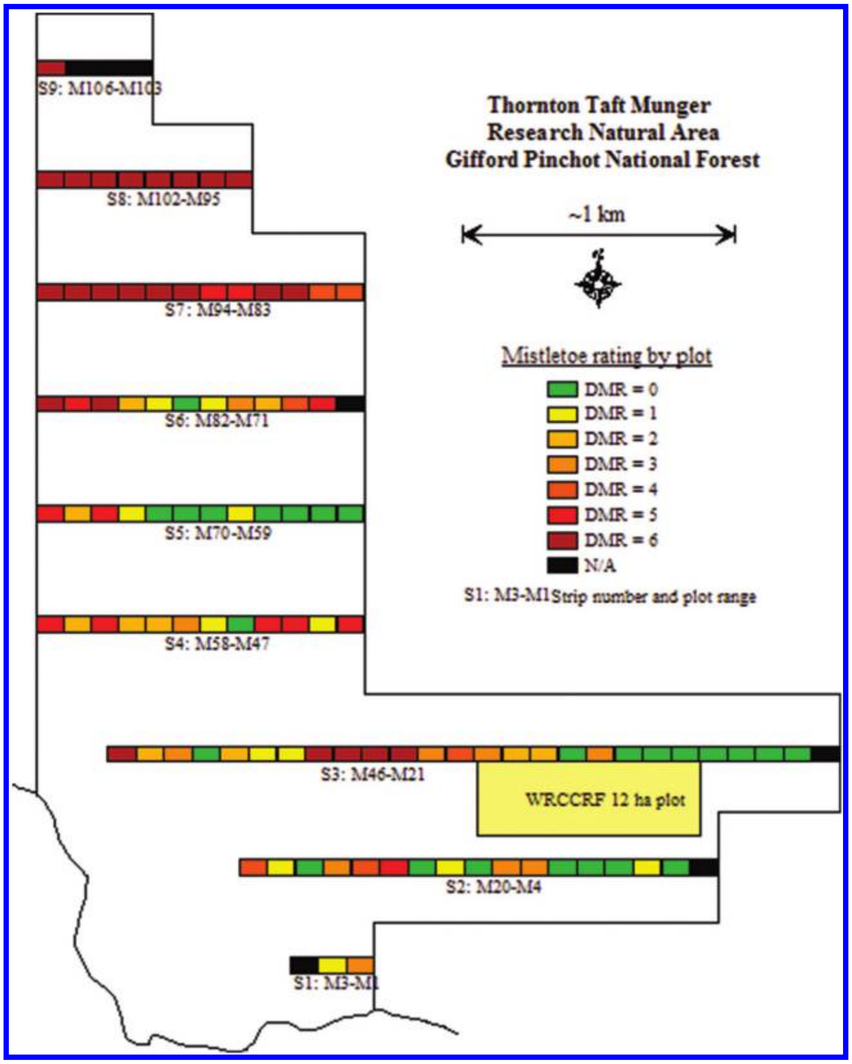
research plot (Fig. 3), which suggests multiple contagion centers. Although mortality associated with dwarf mistletoe was not noted on the research plot, intensification of *A. tsugense* within a large tree crown eventually leads to top dieback, crown decline and mortality (Hennon et al. 2001; Muir and Hennon 2007), as evidenced by dead branches described by Meinzer et al. (2004). In the absence of fire, the clumped nature of the DMR 6 trees could influence fuels organization on the landscape by the development of mortality centers, which would disrupt the continuity of canopy fuels by creating gaps. This would lead to a complex, patchy mixture of fuels due to a high incidence of witches' brooms, dead and declining host trees, and nonhost success in gaps, potentially leading to increased ladder fuels.

Swanson et al. (2006) reported on two additional *A. tsugense* surveys. One survey was conducted in an old-growth forest where they surveyed 1661 *T. heterophylla* trees and documented plot average DMR (Fig. 4). Swanson et al. (2006) found that 83% of the plots had *A. tsugense* present, and that large areas of the northern portion of the forest had a plot average DMR of 6, the maximum possible (Fig. 4). It appears that this is a region of the forest that may have served as refugia for *A. tsugense* and was not completely burned. *Arceuthobium tsugense* then hypothetically spread from several or one refugia into surrounding forests, with the assistance of birds. Shaw et al. (2005) hypothesized that red crossbills (*Loxia curvirostra* Linnaeus), which have a subspecies or biotype that focuses on *T. heterophylla* (Benkman 1993), may be a potential passive vector because they move between *T. heterophylla* individuals in the mid and upper canopy taking seed from cones during the time that *A. tsugense* disperse seed in late September and October (personal observation). It is possible that the explosively discharged seed, which is covered with sticky viscin, could attach to feathers and be dispersed to uninfected trees.

The second survey was conducted in a 157 year old forested watershed that is dominated by *P. menziesii*. Swanson et al. (2006) surveyed the entire watershed using aerial survey, road walks, stream walks, and forest transects. They found that *A. tsugense* was limited to 2.4% of the watershed and was concentrated in riparian areas where *T. heterophylla* survived fire. They found that old-growth trees and snags as well as infected trees were aggregated in these patches. Because *P. menziesii* dominated the surrounding forest at the time of the study, there was no potential for *A. tsugense* to spread outside these patches. Therefore, *A. tsugense* appears to persist on the landscape after fire in unburned or partially burned areas, and does not spread into the adjacent forests that are dominated by *P. menziesii* for over 250 years until *T. heterophylla* becomes abundant.

The epidemiology and spread of *A. tsugense* in this type was informed by several other studies on the 12 ha plot. The sex ratio of *A. tsugense* is 50:50 male–female (Mathiasen and Shaw 1998), and the aerial shoots occur only in the middle and upper canopy above 35 m, the height at which there is a minimum amount of light required for aerial shoot occurrence (Shaw and Weiss 2000). Therefore seed production and dispersal typically comes from the mid and upper canopy, and seed rains down upon *T. heterophylla* as it emerges into the canopy. No bole infections were observed on any trees with a DMR of 6 that were between 40 and 55 m in height, indicating these trees were infected after attaining significant height. Although the *P. menziesii* was 450–500 years old, the maximum age of *T. heterophylla* found on the plot was approximately 250 years. Trees with a DMR of 6 on the site were likely infected over 100–120 years ago based on

Fig. 4. Average dwarf mistletoe rating (range: 0–6) for 0.4 ha (1 acre) plots along transects in the T.T. Munger Research Natural Area. Map by Elizabeth Freeman. Data from Swanson et al. (2006).



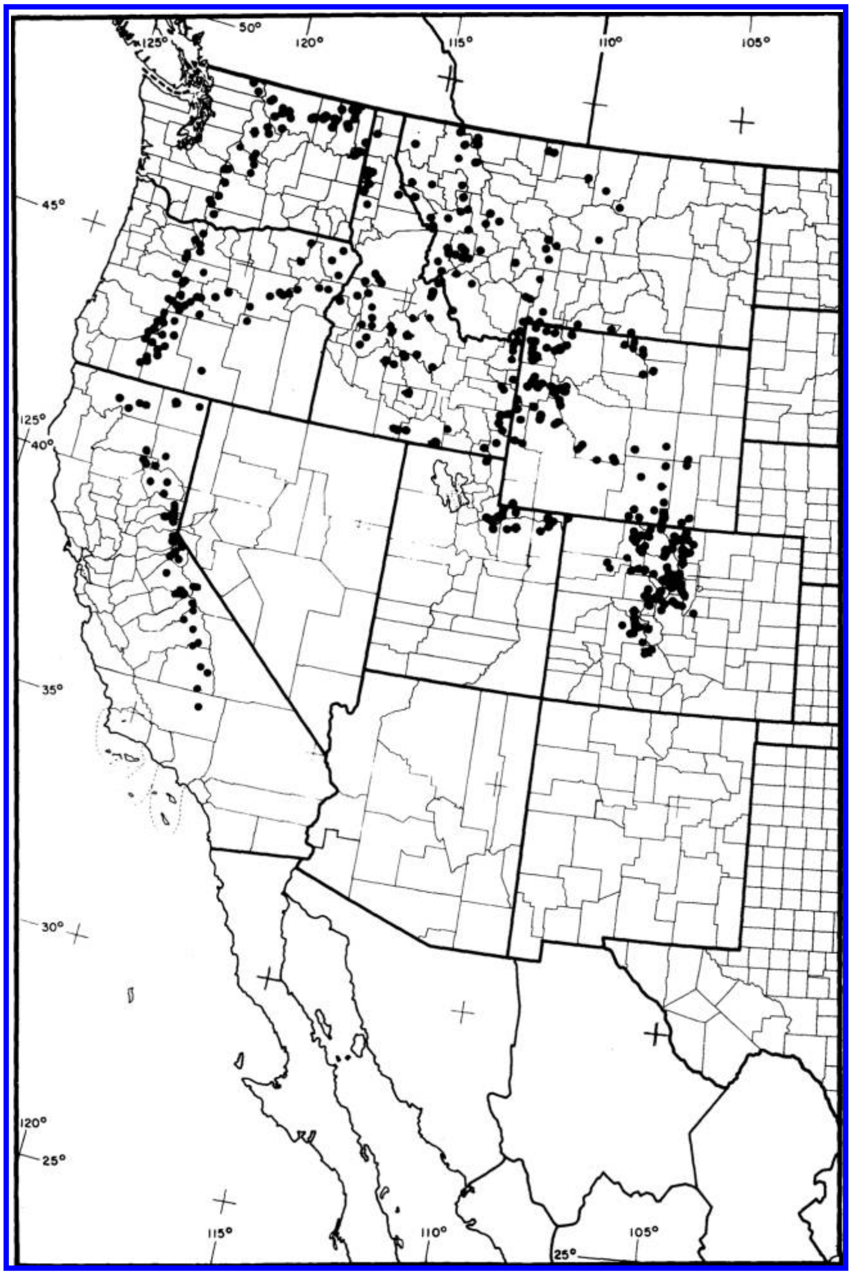
tree ring and stable isotope studies compared to uninfected trees of similar age and size (Marias et al. 2014). Shaw et al. (2005) hypothesized that the seed that initiated the infection centers must have been transported (likely by birds) onto the site from nearby refugia which survived the previous fire. One large infection center is about 120 m wide (Fig. 3) and 120 years old, suggesting composition and structure, especially nonhosts, limited the spread to about 0.5 m per year, even though seed may disperse up to 12 m from host trees (Muir and Hennon 2007). However, as the *P. menziesii* dies out of the stand and *T. heterophylla* increases in abundance, the rate of spread is likely to accelerate.

In the case of the southern Washington Cascades, refugia were of two types: one in riparian zones, and the other in a low density site on very low productivity soils that hypothetically did not burn completely during the previous fire. *Arceuthobium tsugense* is commonly observed on poor or low productivity sites (Muir and Hennon 2007) and we hypothesize that mixed severity fire on these sites results in refugia for the species. Additional sites that may influence creation of refugia could also include locations with many rock outcrops, stands with limited ladder fuels, or stands surrounded by bodies of water. These refugia allow *A. tsugense* to persist during extended periods of nonhost dominance and provide a source of inoculum as hosts establish more widely in the forest.

Lodgepole pine dwarf mistletoe in the lodgepole pine forests of the pumice plateau of south-central Oregon, USA

Lodgepole pine dwarf mistletoe (*Arceuthobium americanum*) is present throughout the range of lodgepole pine (*Pinus contorta*) in North America (Fig. 5; Hawksworth and Wiens 1996). Here, we focus on the south-central Oregon *P. contorta* zone (Franklin and Dyrness 1973), which is ecologically distinct from most other *P. contorta* forests. Within this region, *P. contorta* is typically a climax species as well as early successional colonizer, often existing in monospecific, multi-storied, and uneven-aged stands (Franklin

Fig. 5. Distribution map of *Arceuthobium americanum* in western USA (from Hawksworth and Wiens 1996). Available online at http://www.treesearch.fs.fed.us/pubs/4699.



and Dyrness 1973, Simpson 2007), in contrast with the seral, single-aged stands (eventually succeeding to *Abies* and *Picea* forests), which characterize the majority of the distribution of *P. contorta* in the Rocky Mountains (Lotan et al. 1985). Seral *P. contorta* forests of the Rocky Mountains experience a high severity, stand replacement fire regime and high levels of cone serotiny are common (Lotan and Critchfield 1990), while *P. contorta* forests of south-central Oregon experience a mixed severity fire regime (Agee 1993; Heyerdahl et al. 2014) and infrequent cone serotiny (Mowat 1960; Lotan and Critchfield 1990). We propose that the monospecific, uneven-aged structure and mixed-severity fire regime of south-central Oregon *P. contorta* forests perpetuates *A. americanum* on the landscape.

Arceuthobium americanum's effects on stand structure have been well-documented in *P. contorta* forests. Severe *A. americanum* infection leads to structural changes such as decreased average dominant tree height and diameter, increased regeneration density, and decreased live basal area (Wanner and Tinnin 1989; Godfree et al. 2002*a*; Godfree et al. 2002*b*). In addition, Godfree et al. (2003) showed that live biomass was generally skewed to lower canopy strata in heavily infected stands, compared with lightly infected stands, although height to crown base and total canopy volume did not differ (Godfree et al.

2002*a*). The implications of these structural changes for effects on fuels loadings are equivocal, particularly given that height to crown base and canopy volume, two important fuels components which influence crown fire (Van Wagner 1977), did not change as a result of differences in *A. americanum* severity.

Although individual effects of *A. americanum* on the structure of this forest type are relatively well-understood, they must be examined within the context of other drivers of stand structure to accurately reflect dynamics in these forests. Mountain pine beetle (MPB) is an important driver of stand structure and landscape dynamics of *P. contorta* forests; impacts on fuels structure have been of particular interest over the previous decade (see Hicke et al. 2012, Jenkins et al. 2014 for recent reviews). During a MPB epidemic, the majority of dominant and codominant *P. contorta* in a stand is killed, leaving intermediate, suppressed, and nonhost species (Roe and Amman 1970). However, in south-central Oregon, nonhost species are uncommon in *P. contorta* forests (Simpson 2007). Over time following an epidemic, dead trees drop their needles, snags fall, downed wood accumulates, and previously suppressed trees are released to the overstory (Hicke et al. 2012). Given that MPB and *A. americanum* interact to influence stand structure and fuels loadings, both must be considered together to accurately characterize effects on the landscape.

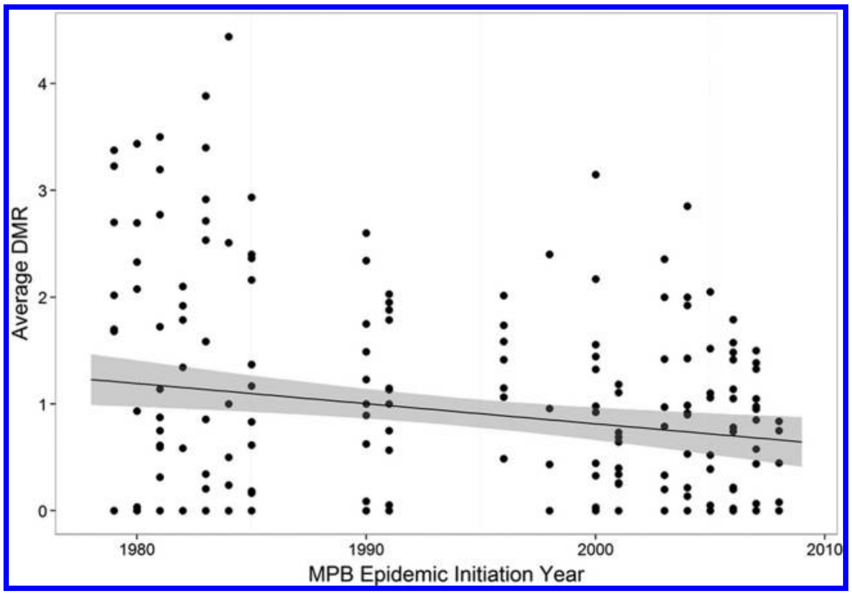
Agne et al. (2014) investigated *A. americanum*'s effects on stand structure following mountain pine beetle activity in old stage (21–28 years after epidemic initiation) *P. contorta* forests. Similar to previous findings, they found decreased average diameter and decreased representation of dominant and codominant trees as *A. americanum* severity increased, as well as increased representation of suppressed trees. However, contrary to previous findings, they found a decrease in canopy volume with increased *A. americanum* severity and no effect on stand density overall. These differences among studies indicate that MPB effects on stand structure may alter the structural effects of *A. americanum*. Conversely, it is also important to take *A. americanum* into account when considering post-MPB forests as it may have a large impact on stand development.

To further investigate the interactions between *A. americanum* and fuels in post-mountain pine beetle *P. contorta* stands in south-central Oregon, we utilized data collected from three previously established plot networks: a mountain pine beetle fuels chronosequence plot network, an old stage mountain pine beetle plot network, and a post-fire plot network. In the summers of 2010 and 2011, we established the mountain pine beetle fuels chronosequence, consisting of 213 plots randomly located across a 30 year period of mountain pine beetle initiation in south-central Oregon *P. contorta*. Plots were established within 19 separate epidemic initiation years, ranging from 2–32 years post-epidemic initiation (Shaw et al. 2014). During the summer of 2012, we established the old stage mountain pine beetle plot network. Thirteen stands sampled in the mountain pine beetle fuels chronosequence, ranging from 21 to 28 years since mountain pine beetle epidemic initiation, were selected for additional intensive sampling of overstory tree structure (Agne et al. 2014). During the summer of 2013, 52 plots were randomly established within the *P. contorta* forests in the 2012 Pole Creek Fire perimeter. All plots had experienced a mountain pine beetle epidemic prior to fire; epidemic initiation occurred 8 to 15 years prior to fire (Agne et al. 2016).

We assessed dwarf mistletoe rating (DMR) using the Hawksworth 6 class rating system (Hawksworth 1977) on each live tree ≥5 cm diameter at breast height (DBH) within a 8.92 m radius plot at each of the chronosequence plots (n = 213), within three 75 m × 10 m belt transects in each of the 13 old-stage stands (n = 39), and within an 11.3 m radius plot at each of the post-fire plots (n = 52). We averaged the DMR of all live trees on each plot to obtain average DMR. Additionally, we counted 1, 10, 100, and 1000 h fuels, and measured litter and duff depth along four 25 m Brown's transects on the chronosequence plots (Brown 1974). Starting at the transect end (i.e., 25 m from plot center), we counted 1, 10, 100, and 1000 h fuels for 2, 5, 10, and 25 m, respectively, on each of the four transects, while litter and duff depths were measured at two points on each transect, 5 and 15 m from plot center. We converted counts of downed woody fuels to biomass using equations from Harmon and Sexton (1996), coarse fuels density values for lodgepole pine from Busse (1994), and fine fuels density values and coarse fuel density values for all other species from Harmon et al. (2008). Litter and duff depths were converted to biomass using equations from Lutes et al. (2006). We also measured heights of saplings (trees ≥ 40 cm in height and <5 cm DBH) and shrubs (subsequently referred to as ladder fuels) within four 3.2 m radius plots at each chronosequence plot. Additional information on the methods used to establish the chronosequence plot network are available in Shaw et al. (2014). Measurements also taken in the old stage plot network were height, height to crown base, DBH, and crown radii in four directions for each live tree ≥ 5 cm DBH within three 75 m × 10 m belt transects per stand. Information on the methods used to collect data in the old stage plot network is available in Agne et al. (2014). Canopy base height and canopy bulk density, fuels components that influence crown fire behavior, were calculated in FuelCalc version 0.52 (Reinhardt et al. 2006) and statistical analyses were performed in R version 3.1 (R Core Team 2014).

Given that mountain pine beetle epidemics have a profound effect on fuel loadings over time, dwarf mistletoe effects on fuels in lodgepole pine must be examined within the context of mountain pine beetle impacts. To

Fig. 6. Linear model of the effect of mountain pine beetle (MPB) epidemic initiation year on average dwarf mistletoe rating (DMR) with 95% confidence intervals.



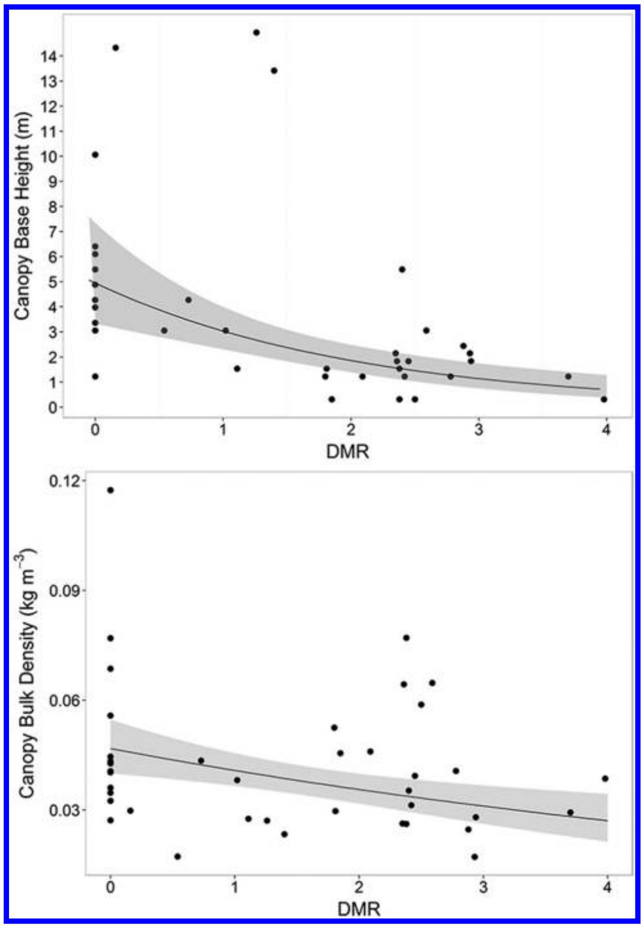
address the question: "How does *A. americanum* severity change following a mountain pine beetle epidemic?" we compared average DMR across MPB initiation years with a linear model using the chronosequence data. We hypothesized that average DMR would decrease with decreasing time since MPB epidemic initiation (hereinafter, time since beetle), given that MPB causes mortality of *A. americanum* host trees. This hypothesis was supported ($F_{[1,211]} = 8.612$, $p = 0.004$). However, estimated average DMR decreased by only 0.02 with each year of decreasing time since beetle and there was a high level of variability around this relationship ($r^2 = 0.04$, Fig. 6). *Arceuthobium americanum* remained abundant overall following MPB; it was present on over 70% of the plots within the chronosequence, with an overall average DMR of 1.3 across all MPB epidemic initiation years. Its continued dominance within these disturbed stands is likely due to the presence of *A. americanum* in intermediate and suppressed *P. contorta*, generally unsuitable hosts for mountain pine beetle, following an epidemic (Roe and Amman 1970). *Arceuthobium americanum* levels prior to the mountain pine beetle epidemic are unknown, but it is clear that MPB does not typically sanitize south-central Oregon *P. contorta* stands of *A. americanum* following an epidemic.

We used data collected in the old-stage MPB plot network to determine the effects of *A. americanum* on canopy fuels, while controlling for stage of post-MPB development. To understand effects of *A. americanum* on surface and ladder fuels within the same stage, we used a subset of the chronosequence data (MPB initiation years 1984–1991). We used linear mixed models to model the relationship of average DMR to canopy base height and canopy bulk density; both variables were log-transformed to meet model assumptions. Additionally, we used BIC to select from candidate models which included combinations of productivity level, MPB mortality level, and stand density as covariates. Model selection indicated that the inclusion of stand density as a covariate in the canopy bulk density model was appropriate, and no covariates were included in the canopy base height model. We used linear models to model the relationship of average DMR to the surface fuels characteristics 1, 10, 100, and 1000 h fuel biomass, and litter and duff biomass as well as the ladder fuels characteristics average and maximum sapling height, and average and maximum shrub height. Litter and duff biomass, average sapling height, and average shrub height were log-transformed to meet model assumptions. All statistical analyses were performed in R version 3.1 (R Core Team 2014).

Within old-stage MPB stands, average DMR had a strong effect on canopy base height ($F_{[1,25]} = 11.25$, $p = 0.0025$); median canopy base height was estimated to decrease 35.2% (95% CI: 15.4%–50.4%) for each unit increase in DMR (Fig. 7). The effect of DMR on canopy bulk density was equivocal ($F_{[1,24]} = 3.376$, $p = 0.078$), with an estimated 12.8% (95% CI: 4.9%, 19.8%) decrease in the median canopy bulk density for each unit increase in DMR after accounting for stand density (Fig. 7). Average DMR had little effect on surface and ladder fuels in old-stage MPB stands (Table 1) as none of these relationships were significant at the $\alpha = 0.05$ level.

Canopy base height is one of the primary fuels attributes that drives torching (passive crown fire) potential (Van Wagner 1977). Ladder fuels, such as regeneration and woody shrubs, also play a role in the transition of a fire from surface to crown (Agee and Skinner 2005; Heyerdahl et al. 2014). Given that increases in average DMR led to substantial decreases in canopy base height, while ladder fuel height did not change, *A. americanum* likely plays a key role in driving passive crown fire

Fig. 7. Linear mixed model results of canopy fuels' responses to increased average dwarf mistletoe rating (DMR) with 95% confidence intervals. Log-transformed responses are reported on the original scale.



potential. It should be noted, however, that this relationship is theoretical and further research is needed to discern *A. americanum*'s effects on in situ fire behavior. The possible decrease in canopy bulk density with increased average DMR is likely related to decreased representation of dominant and codominant trees (Agne et al. 2014) as most of a stand's canopy bulk density is in larger trees. However, it should be noted that the range of canopy bulk density observed in this study was very low (under 0.1 kg·m^{-3} with the exception of one plot). Given these extremely low values, it is unlikely that dwarf mistletoe plays a large role in active crown fire behavior in these forests. Surface fuels were also largely unaffected by *A. americanum*. Despite previous evidence that dwarf mistletoe increases surface fuel loadings in other forest types (Hoffman et al. 2007; Stanton and Hadley 2010), we attribute the general lack of a relationship in this system to the larger-scale impacts from mountain pine beetle, and the large amount of variability which has been shown to be associated with such large-scale disturbances in various forest types (Donato et al. 2013; Agne et al. 2016).

Table 1. Linear model results of surface and ladder fuels' responses to increased dwarf mistletoe rating (DMR).

	95% CI				
Variable	Effect size	SE[a]	Lower[a]	Upper[a]	*P* value
Surface fuels					
1 h fuel load (Mg)[a]	0.10	0.08	−0.05	0.26	0.20
10 h fuel load (Mg)[a]	0.30	0.16	−0.02	0.63	0.07
100 h fuel load (Mg)[a]	0.25	0.41	−0.58	1.07	0.55
1000 h fuel load (Mg)[a]	2.07	2.18	−2.35	6.49	0.35
Litter and duff biomass (Mg)[b]	0.94	—	0.85	1.03	0.16
Ladder fuels					
Maximum sapling height (cm)[a]	0.03	0.05	−0.07	0.13	0.53
Average sapling height (cm)[b]	0.97	—	0.90	1.03	0.31
Maximum shrub height (cm)[a]	−6.91	4.53	−16.11	2.28	0.14
Average shrub height (cm)[b]	1.00	—	0.89	1.13	0.95

[a] Effect sizes, standard errors (SE), and 95% confidence intervals (CI) represent the change in fuel load associated with a single unit increase in average DMR.

[b] Models were log transformed; effect sizes, 95% CI represent multiplicative effects associated with a single unit increase in average DMR.

We used the post-fire plot network to investigate the effects of mountain pine beetle and fire on *A. americanum* abundance within the Pole Creek Fire perimeter. We did not have estimates of *A. americanum* from the Pole Creek Fire perimeter prior to the fire, so we used the MPB chronosequence data from epidemic initiation years 1997–2004 as a proxy for pre-fire data to determine the effects of these two disturbances on *A. americanum*. As we expected, the percentage of total plots with *A. americanum* was lower within the fire perimeter than in the chronosequence plot network (Table 2). Similarly, the average DMR observed in the post-fire plot network was lower than that of the chronosequence plot network (Table 2). However, when post-fire plots were restricted to only those which had live trees (51% of total plots), *A. americanum* was present on 77.8% of plots, which is comparable to pre-fire estimates of *A. americanum* incidence in this area (Agne et al. 2014). Plots which contained live trees generally represented plots which had experienced low severity fire, and severity was found to be lower in plots with high levels of prior MPB mortality (Agne et al. 2016). Therefore, within the post-fire environment, there should be a positive relationship between pre-fire MPB mortality and *A. americanum* incidence where *A. americanum* was present prior to fire, because areas with low severity MPB burned more severely.

Arceuthobium americanum appears to be controlled by fire in the *P. contorta* forests of south-central Oregon. However, the mixed severity fire regime leads to reductions in stand level DMR, but not eradication from

Table 2. Dwarf mistletoe incidence and severity in MPB chronosequence (pre-fire) plots, all post-fire plots, and post-fire plots with live trees only.

	MPB chronosequence plots (attacked 1997–2004)	All post-fire plots	Post-fire plots with live trees
Plots with dwarf mistletoe	71.4%	40.4%	77.8%
Average stand DMR	0.77	0.28	0.55
Stand DMR range	0–3.14	0–2.36	0–2.36

landscapes, as would be expected in forests with stand replacement fire regimes. Unburned and low severity patches within fires likely serve as sources for reinvasion of areas which were sanitized of *A. americanum* following a burn. However, *P. contorta* colonizes sites following fire, so *A. americanum* hosts remain generally pervasive on the landscape and reinvasion of sites can occur relatively quickly. *Arceuthobium americanum* may also contribute to the existence of a mixed severity fire regime by influencing canopy fuels in heavily infected stands and generally contributing to heterogeneity on the landscape. Furthermore, *A. americanum* interacts with mountain pine beetle to influence fuels and forest structure, as it is prevalent across post-mountain pine beetle forests.

Conclusions and future research needs

Fire significantly influences the occurrence and epidemiology of dwarf mistletoes in the forests of western North America, except in hypermaritime coastal rainforests where fire is extremely rare. Comparing the fire ecology of *A. tsugense* with *A. americanum* provides insight into dwarf mistletoe population dynamics on the landscape in fire prone forests and emphasizes the importance of fire in dwarf mistletoe ecology. *Arceuthobium* spp. ecology appears to be driven by an interwoven interaction of spatial landscape patterns of current infection centers, dwarf mistletoe influence on subsequent fire behavior, fire severity influence on dwarf mistletoe survival, and the complex interactions with other disturbance agents in the forest. Refugia, or areas that do not burn completely, provide a place for dwarf mistletoe to persist and then spread.

Arceuthobium americanum's interactions with fire differ from those of *A. tsugense* primarily because of the successional characteristics of their hosts. *Pinus contorta* is an early successional species that recolonizes burned areas directly adjacent to refugia, whereas *T. heterophylla* may not become common in a *P. menziesii* forest for 200 or more years. Thus, *A. americanum* can immediately begin spreading from refugia, whereas *A. tsugense* must persist locally for many years. The successional status of the host was deemed of primary significance to understanding the interactions of fire and dwarf mistletoe by Wicker and Leaphart (1974), who also concluded that some tree species, such as *P. contorta*, can be either early-successional or persist as late-successional species. *Arceuthobium americanum* epidemiology and ecology likely differs between early-successional and persistent *P. contorta*. Successional characteristics are linked to fire regime characteristics, therefore interactions between fire and dwarf mistletoes may be highly variable, necessitating further research in various fire-prone forest types with dwarf mistletoes.

There are many gaps in our knowledge of fire and dwarf mistletoe interactions in western North America. Additional research is needed regarding the effects of dwarf mistletoe on fuels, particularly in fuels loadings at the stand scale in forest types other than ponderosa pine. However, further research on dwarf mistletoe's effect on branch-level fuels attributes related to witches' brooms may be of highest importance. Specifically, branch-level influence of dwarf mistletoe on crown bulk density must be resolved to appropriately model dwarf mistletoe's influence on canopy bulk density, as current models assume that the allometric equations used to model healthy trees are applicable to heavily infected trees with witches' brooms.

There are also gaps in knowledge surrounding the influence of dwarf mistletoe on fire behavior. Little empirical evidence exists surrounding dwarf mistletoe effects on fire behavior, so we suggest that additional prescribed burning in various forest types, with variable levels of dwarf mistletoe, would be highly beneficial to understanding this relationship. Studies incorporating measurement of pre-fire forest condition, real-time fire behavior, and post-fire patterns of fire severity and fire effects in forests with *Arceuthobium* infection centers would be particularly beneficial to understanding the ways in which dwarf mistletoe and fire interact. Mixed and high severity fire regimes may be influenced by landscape patterns associated with well-developed infection centers. These findings could then be compared with results from fire behavior models, and the models could be improved for use in stands with dwarf mistletoe. Dwarf mistletoe effects on post-fire tree survival should also be investigated in prescribed burns in forest types other than ponderosa pine, as these effects likely vary with forest structure and species tolerance to fire.

In conclusion, the interactions between *Arceuthobium* spp. and fire are integral to the ecology of western North American dry forests. Although disturbance interactions in these systems have received increasing attention in recent years, dwarf mistletoes are rarely included. Given their prevalence on the landscape and the magnitude of their effects, we feel that their inclusion is warranted in future studies in this region.

Acknowledgements

We acknowledge Joint Fire Science Program Grant No. 09-1-06-17 and USDA Forest Service Forest Health Monitoring Evaluation Monitoring project WC-EM-F-13-03, which supported data collection in central Oregon. The Richard Strachan Fellowship, Western Wildland Environmental Threat Assessment Center also funded a portion of this research. We especially thank Travis Woolley and Stephen Fitzgerald for work and project design on the Joint Fire Science and Forest Health Monitoring projects. We thank Duncan Galvin, Paul Gress, Joey Hulbert, Amanda Lee, Mailea Miller-Pierce, Monica Queijeiro-Bolaños, Katie Rigsby, and Marcia Rosenquist for assistance with data collection in central Oregon. Thanks to Liz Freeman for creating Figs. 3 and 4.

References

Agee, J.K. 1993. Fire ecology of Pacific Northwest forests. Island Press, Washington, D.C.

Agee, J.K., and Skinner, C.N. 2005. Basic principles of forest fuel reduction treatments. For. Ecol. Manage. **211**: 83–96. doi:10.1016/j.foreco.2005.01.034.

Agne, M.C., Shaw, D.C., Woolley, T.J., and Queijeiro-Bolaños, M.E. 2014. Effects of dwarf mistletoe on stand structure of lodgepole pine forests 21–28 years post-mountain pine beetle epidemic in central Oregon. PLoS ONE, **9**: e107532. [Online.] doi:10.1371/journal.pone.0107532. PMID:25221963.

Agne, M.C., Woolley, T., and Fitzgerald, S. 2016. Fire severity and cumulative disturbance effects in the post-mountain pine beetle lodgepole pine forests of the Pole Creek Fire. For. Ecol. Manage. **366**: 73–86. doi:10.1016/j.foreco.2016.02.004.

Alexander, M.E., and Hawksworth, F.G. 1975. Wildlfand fires and dwarf mistletoes: a literature review of ecology and prescribed burning. USDA For. Serv. Gen. Tech. Rep. RM-14.

Alexander, M.E., and Hawksworth, F.G. 1976. Fire and dwarf mistletoes in North American coniferous forests. J. For. **74**(7): 446–449.

Allen, C.D., Breshears, D.D., and McDowell, N.G. 2015. On underestimation of global vulnerability to tree mortality and forest die-off from hotter drought in the Anthropocene. Ecosphere, **6**(8): 129. doi:10.1890/ES15-00203.1.

Benkman, C.W. 1993. Adaptation to single resources and the evolution of Crossbill (*Loxia*) diversity. Ecol. Monogr. **63**: 305–325. doi:10.2307/2937103.

Brown, J.K. 1974. Handbook for inventorying downed woody material. USDA For. Serv. Gen. Tech. Rep. INT-16.

Busse, M.D. 1994. Downed bole-wood decomposition in lodgepole pine forests of central Oregon. Soil Sci. Soc. Am. J. **58**: 221–227. doi:10.2136/sssaj1994.03615995005800010033x.

Chen, J., Song, B., Rudnicki, M., Moeur, M., Bible, K., North, M., Shaw, D.C., Franklin, J.F., and Braun, D.M. 2004. Spatial relationship of biomass and species distribution in an old-growth *Pseudotsuga-Tsuga* forest. For. Sci. **50**(3): 364–375.

Conklin, D.A., and Geils, B.W. 2008. Survival and sanitation of dwarf mistletoe-infected ponderosa pine following prescribed underburning. W. J. Appl. For. **23**(4): 216–222.

Cruz, M.G., and Alexander, M.E. 2010. Assessing crown fire potential in coniferous forests of western North America: a critique of current approaches and recent simulation studies. Int. J. Wildl. Fire, **19**: 377–398. doi:10.1071/WF08132.

Donato, D.C., Harvey, B.J., Romme, W.H., Simard, M., and Turner, M.G. 2013. Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. Ecol. Appl. **23**(1): 3–20. doi:10.1890/12-0772.1. PMID: 23495632.

Franklin, J.F., and Dyrness, C.T. 1973. Natural vegetation of Oregon and Washington. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-8.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., and Chen, J. 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manage. **155**: 399–423. doi:10.1016/S0378-1127(01)00575-8.

Geils, B.W., Tovar, J.C., and Moody, B. (*Technical editors*). 2002. Mistletoes of North American conifers. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-98.

Geiszler, D.R., Gara, R.I., Driver, C.H., Gallucci, V.F., and Martin, R.E. 1980. Fire, fungi, and beetle influences on a lodgepole pine ecosystem of south-central Oregon. Oecologia, **46**(2): 239–243. doi:10.1007/BF00540132.

Godfree, R.C., Tinnin, R.O., and Forbes, R.B. 2002*a*. The effects of dwarf mistletoe, witches' brooms, stand structure, and site characteristics on the crown architecture of lodgepole pine in Oregon. Can. J. For. Res. **32**(8): 1360–1371. doi:10.1139/x02-058.

Godfree, R.C., Tinnin, R.O., and Forbes, R.B. 2002*b*. Relationships between *Arceuthobium americanum* and the structure of *Pinus contorta* var. *murrayana* stands in central Oregon. Plant Ecol. **165**(1): 69–84. doi:10.1023/A:1021598712920.

Godfree, R.C., Tinnin, R.O., and Forbes, R.B. 2003. Relationships between dwarf mistletoe and the canopy structure of an old-growth lodgepole pine forest in central Oregon. Can. J. For. Res. **33**(6): 997–1009. doi:10.1139/x03-024.

Harmon, M.E., and Sexton, J. 1996. Guidelines for measurements of woody detritus in forest ecosystems. U.S. Long-Term Ecological Research (LTER) Network Publication No. 20. U.S. LTER Network Office, University of Washington, Seattle, Wash.

Harmon, M.E., Woodall, C.W., Fasth, B., and Sexton, J. 2008. Woody detritus density and density reduction factors for tree species in the United States: a synthesis. USDA For. Serv. Gen. Tech. Rep. NRS-GTR-29.

Harrington, M.G., and Hawksworth, F.G. 1990. Interactions of fire and dwarf mistletoe on mortality of southwestern ponderosa pine. USDA For. Serv. Gen. Tech. Rep. RM-191. pp. 234–240.

Hawksworth, F.G. 1961. Dwarfmistletoe of ponderosa pine in the Southwest. USDA For. Serv. Tech. Bull. 1246.

Hawksworth, F.G. 1977. The 6-class dwarf mistletoe rating system. USDA For. Serv. Gen. Tech. Rep. RM-48.

Hawksworth, F.G., and Johnson, D.W. 1989. Biology and management of dwarf mistletoe in lodgepole pine in the Rocky Mountains. USDA For. Serv. Gen. Tech. Rep. RM-169.

Hawksworth, F.G., and Wiens, D. 1996. Dwarf mistletoes: biology, pathology, and systematics. Agricultural Handbook 709. U.S. Dept. of Agriculture, Forest Service, Washington, D.C.

Hennon, P.E., Beatty, J.S., and Hildebrand, D. 2001. Hemlock dwarf mistletoe. USDA For. Serv. Forest Insect and Disease Leaflet (FIDL) 135. R6-NR-FID-PR-01-01.

Hessburg, P.F., Povak, N.A., and Salter, R.B. 2008. Thinning and prescribed fire effects on dwarf mistletoe severity in an eastern Cascade Range dry forest, Washington. For. Ecol. Manage. **255**: 2907–2915. doi:10.1016/j.foreco.2008.01.066.

Heyerdahl, E.K., Loehman, R.A., and Falk, D.A. 2014. Mixed-severity fire in lodgepole pine dominated forests: are historical regimes sustainable on Oregon's Pumice Plateau, USA? Can. J. For. Res. **44**(6): 593–603. doi:10.1139/cjfr-2013-0413.

Hicke, J.A., Johnson, M.C., Hayes, J.L., and Preisler, H.K. 2012. Effects of bark beetle-caused tree mortality on wildfire. For. Ecol. Manage. **271**: 81–90. doi:10.1016/j.foreco.2012.02.005.

Hoffman, C., Mathiasen, R., and Sieg, C.H. 2007. Dwarf mistletoe effects on fuel loadings in ponderosa pine forests in northern Arizona. Can. J. For. Res. **37**(3): 662–670. doi:10.1139/X06-259.

Irving, F.D., and French, D.W. 1971. Control by fire of dwarf mistletoe in black spruce. J. For. **69**: 28–30.

Jenkins, M.J., Runyon, J.B., Fettig, C.J., Page, W.G., and Bentz, B.J. 2014. Interactions among the mountain pine beetle, fires, and fuels. For. Sci. **60**(3): 489–501. doi:10.5849/forsci.13-017.

Kipfmueller, K.F., and Baker, W.L. 1998. Fires and dwarf mistletoe in a Rocky Mountain lodgepole pine ecosystem. For. Ecol. Manage. **108**: 77–84. doi:10.1016/S0378-1127(98)00217-5.

Klutsch, J.G., Beam, R.D., Jacobi, W.R., and Negrón, J.F. 2014. Bark beetles and dwarf mistletoe interact to alter downed woody material, canopy structure, and stand characteristics in northern Colorado ponderosa pine. For. Ecol. Manage. **315**: 63–71. doi:10.1016/j.foreco.2013.12.024.

Koonce, A.L., and Roth, L.F. 1980. The effects of prescribed burning on dwarf mistletoe in ponderosa pine. *In* Proceedings of the Sixth Conference on Fire and Forest Meteorology, Seattle, Wash., 22–24 April 1980. Society of American Foresters, Washington, D.C. pp. 197–203.

Koonce, A.L., and Roth, L.F. 1985. The effects of dwarf mistletoe on fuel in precommercial ponderosa pine stands. *In* Proceedings of the Eighth Conference on Fire and Forest Meteorology, Detroit, Mich., 29 April – 2 May 1985. *Edited by* L.R. Donoghue and R.E. Martin. Society of American Foresters, Bethesda, Md. pp. 66–72.

Lotan, J.E., and Critchfield, W.B. 1990. Lodgepole pine (*Pinus contorta* Douglas. Ex. Loud.). *In* Silvics of North America: 1: Conifers. USDA For. Serv. Agriculture Handbook 654. *Edited by* R.M. Burns and B.H. Honkala.

Lotan, J., Brown, J., and Neuenschwander, L. 1985. Role of fire in lodgepole pine forests. *In* Lodgepole Pine the Species and its Management Symposium Proceedings, Spokane, Wash., and Vancouver, B.C., 8–16 May 1984. *Edited by* D.M. Baumgartner, R.G. Krebill, J.T. Arnott, and G.F. Weetman. pp. 133–152.

Lutes, D.C., Keane, R.E., Caratti, J.F., Key, C.H., Benson, N.C., and Sutherland, S. 2006. FIREMON: fire effects monitoring and inventory system. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-164-CD.

Maloney, P.E., Smith, T.F., Jensen, C.E., Innes, J., Rizzo, D.M., and North, M.P. 2008. Initial tree mortality and insect and pathogen response to fire and thinning restoration treatments in an old-growth mixed-conifer forest of the Sierra Nevada, California. Can. J. For. Res. **38**(12): 3011–3020. doi:10.1139/X08-141.

Marias, D.E., Meinzer, F.C., Woodruff, D.R., Shaw, D.C., Voelker, S.L., Brooks, J.R., Lachenbruch, B., Falk, K., and McKay, J. 2014. Impacts of dwarf mistletoe on the physiology of host *Tsuga heterophylla* trees as recorded in tree ring C and O stable isotopes. Tree Physiol. **34**(6): 595–607. doi:10.1093/treephys/tpu046. PMID:24973917.

Mathiasen, R.L., and Shaw, D.C. 1998. Adult sex ratio of western hemlock dwarf mistletoe at the Wind River Canopy Crane Research Facility, Washington. Madroño, **45**: 210–214.

Mathiasen, R.L., Nickrent, D.L., Shaw, D.C., and Watson, D.M. 2008. Mistletoes: pathology, systematics, ecology, and management. Plant Dis. **92**(7): 988–1006. doi:10.1094/PDIS-92-7-0988.

Meinzer, F.C., Woodruff, D.R., and Shaw, D.C. 2004. Integrated responses of hydraulic architecture, water and carbon relations of western hemlock to dwarf mistletoe infection. Plant Cell Environ. **27**: 937–946. doi:10.1111/j.1365-3040.2004.01199.x.

Mowat, E.L. 1960. No serotinous cones on central Oregon lodgepole pine. J. For. **58**: 118–119.

Muir, J.A., and Hennon, P.E. 2007. A synthesis of the literature on the biology, ecology, and management of western hemlock dwarf mistletoe. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-718.

Muraro, S.J. 1978. Prescribed fire – a tool for the control of dwarf mistletoe in lodgepole pine. *In* Proceedings of the Symposium on Dwarf Mistletoe Control through Forest Management, Berkeley, Calif., 11-13 April 1978. USDA For. Serv. Gen. Tech. Rep. PSW-31. *Technical coordinators* R.F. Scharpf and J.R. Parmeter, Jr. pp. 124–127.

Parker, T.J., Clancy, K.M., and Mathiasen, R.L. 2006. Interactions among fire, insects and pathogens in coniferous forests of the interior western United States and Canada. Agric. For. Entomol. **8**(3): 167–189. doi:10.1111/j.1461-9563.2006.00305.x.

Queijeiro-Bolaños, M.E., Cano-Santana, Z., and Castellanos-Vargas, I. 2013. Does disturbance determines the prevalence of dwarf mistletoe (*Arceuthobium*, Santalales: Viscaceae) in Central Mexico? Rev. Chil. Hist. Nat. **86**: 181–190. doi:10.4067/S0716-078X2013000200007.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. [Online.] Available from https://www.R-project.org [accessed 18 August 2016].

Reinhardt, E., Lutes, D., and Scott, J. 2006. FuelCalc: a method for estimating fuel characteristics. *In* Fuels Management—How to Measure Success: Conference Proceedings, Portland, Ore., 28-30 March 2006. *Edited by* P.L. Andrews and B.W. Butler. pp. 273–282.

Roe, A.L., and Amman, G.D. 1970. The mountain pine beetle in lodgepole pine forests. USDA For. Serv. Res. Pap. INT-71.

Roth, L.F. 1953. Pine dwarf mistletoe on the Pringle Falls Experimental Forest. USDA For. Serv. Res. Note 91.

Sala, A., Carey, E.V., and Callaway, R.M. 2001. Dwarf mistletoe affects whole-tree water relations of Douglas fir and western larch primarily through changes in leaf to sapwood ratios. Oecologia, **126**: 42–52. doi:10.1007/s004420000503.

Shaw, D.C., and Greene, S. 2003. Focus on field stations: Wind River Canopy Crane Research Facility and Wind River Experimental Forest. Bull. Ecol. Soc. Am. **83**: 115–121.

Shaw, D.C., and Weiss, S.B. 2000. Canopy light and the distribution of hemlock dwarf mistletoe (*Arceuthobium tsugense* (Rosendahl) G.N. Jones ssp. *tsugense*) aerial shoots in an old-growth Douglas-fir/western hemlock forest. Northw. Sci. **74**(4): 306–315.

Shaw, D.C., Watson, D.M., and Mathiasen, R.L. 2004*a*. Comparison of dwarf mistletoes (*Arceuthobium* spp., Viscaceae) in the western United States with mistletoes (*Amyema* spp., Loranthaceae) in Australia — ecological analogs and reciprocal models for ecosystem management. Aust. J. Bot. **52**: 481–498. doi:10.1071/BT03074.

Shaw, D.C., Franklin, J.F., Bible, K., Klopatek, J., Freeman, E., Greene, S., and Parker, G.G. 2004*b*. Ecological setting of the Wind River old-growth forest. Ecosystems, **7**(5): 427–439. doi:10.1007/s10021-004-0135-6.

Shaw, D.C., Chen, J., Freeman, E.A., and Braun, D.M. 2005. Spatial and population characteristics of dwarf mistletoe infected trees in an old-growth Douglas-fir – western hemlock forest. Can. J. For. Res. **35**(4): 990–1001. doi:10.1139/x05-022.

Shaw, D.C., Oester, P.T., and Filip, G.M. 2009. Managing insects and diseases of Oregon conifers. Oregon State University Extension Manual 8980. Corvallis, Oregon. Available from https://catalog.extension.oregonstate.edu/ [accessed 29 November 2016].

Shaw, D., Hollingsworth, L., Woolley, T., Fitzgerald, S., Eglitis, A., and Kurth, L. 2014. Fuel dynamics and potential fire behavior in lodgepole pine following mountain pine beetle epidemics in south-central Oregon. [Online.] Joint Fire Science Program Final Report 09-1-06-17, Joint Fire Science Program, Boise, I.D. Available from https://www.firescience.gov/projects/09-1-06-17/project/09-1-06-17_final_report.pdf [accessed 18 August 2016].

Simpson, M. 2007. Forested plant associations of the Oregon East Cascades. USDA For. Serv. Tech. Pap. R6-NR-ECOL-TP-03-2007.

Stanton, S. 2009. Western dwarf mistletoe and prescribed fire behavior — a case study from Crater Lake National Park. Northw. Sci. **83**(3): 189–199. doi:10.3955/046.083.0303.

Stanton, S., and Hadley, K.S. 2010. Influence of western dwarf mistletoe (*Arceuthobium campylopodum* Engelm.) on surface fuels and snag abundance in mature ponderosa pine and mixed conifer stands in central Oregon. Nat. Areas J. **30**(3): 261–270. doi:10.3375/043.030.0302.

Swanson, M.E., Shaw, D.C., and Marosi, T.K. 2006. Distribution of western hemlock dwarf mistletoe (*Arceuthobium tsugense* [Rosendahl] G.N. Jones subsp. *tsugense*) in mature and old-growth Douglas-fir (*Pseudotsuga menziesii* [Mirb.] Franco) forests. Northw. Sci. **80**(3): 207–217.

Trummer, L.M., Hennon, P.E., Hansen, E.M., and Muir, P.S. 1998. Modeling the incidence and severity of hemlock dwarf mistletoe in 110-year-old wind-disturbed forests in southeast Alaska. Can. J. For. Res. **28**(10): 1501–1508. doi:10.1139/x98-132.

Turner, M.G., Romme, W.H., and Gardner, R.H. 1999. Prefire heterogeneity, fire severity, and early postfire plant reestablishment in subalpine forests of Yellowstone National Park, Wyoming. Int. J. Wildl. Fire, **9**(1): 21–36. doi:10.1071/WF99003.

Van Wagner, C.E. 1977. Conditions for the start and spread of crown fire. Can. J. For. Res. **7**(1): 23–34. doi:10.1139/x77-004.

Wanner, J.L., and Tinnin, R.O. 1989. Some effects of infection by *Arceuthobium americanum* on the population dynamics of *Pinus contorta* in Oregon. Can. J. For. Res. **19**(6): 736–742. doi:10.1139/x89-113.

Wicker, E.F., and Leaphart, C.D. 1974. Fire and dwarf mistletoe (*Arceuthobium* spp.) relationships in the Northern Rocky Mountains. *In* Proceedings, Tall Timbers Fire Ecology Conference, Fire and Land Management Symposium, Missoula, Mont., Tallahassee, Fla., 8–10 October 1974. pp. 279–298.

Zimmerman, G.T., and Laven, R.D. 1984. Ecological interrelationships of dwarf mistletoe and fire in lodgepole pine forests. *In* Biology of Dwarf Mistletoes: Proceedings of the Symposium, Fort Collins, Colo., 8 August 1984. *Edited by* F.G. Hawksworth and R.F. Scharpf. pp. 123-131.

Zimmerman, G.T., and Laven, R.D. 1987. Effects of forest fuel smoke on dwarf mistletoe seed germination. Gt. Basin Nat. **47**(4): 652–659.